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Aspects of Histocompatibility and Regeneration in the Solitary Reef Coral *Fungia scutaria*

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Abstract. Discoid coralla of the solitary free-living reef coral *Fungia scutaria* were cut with a rock saw and rejoined in various paired combinations and orientations of autogeneic sections (self to self), isogeneic sections (clone-mate to clone-mate), and allogeneic sections (two different genotypes). Results of these experiments provide the first evidence of histocompatibility in a solitary coral. Autogeneic or isogeneic sections of coralla with one section containing a mouth were joined along cut edges. In all cases, fusion of tissues occurred within weeks, followed by skeletal fusion within months. However, autogeneic or isogeneic sections rejoined along the uncut edges did not fuse. Isogeneic pairings between two sections with mouths produced neither tissue/skeletal fusion nor cytotoxicity at the interface. Individual cut sections were allowed to regenerate. Sections containing the parent mouth did not develop new mouths. However, cut sections lacking a mouth always regenerated multiple mouths along the cut edge, but not along the uncut edge. Sections without mouths cut along a second line parallel to the first cut always regenerated mouths along the cut edge located closest to what had been the mouth area of the original corallum. The new mouths eventually developed into individual polyps.

Introduction

Studies over the last two decades have shown generalized self/not-self recognition in coelenterates (Hildemann *et al.*, 1975a, 1975b, 1977; Grosberg, 1988; Bigger, 1988). Aside from sea anemones, most studies of anthozoan histoincompatibility have involved colonial species (Grosberg, 1988). Among the scleractinia, colonial corals have been used as experimental subjects. Previous attempts to demonstrate allogeneic and isogeneic reactions in solitary reef corals failed to produce a response. For example, the solitary coral *Fungia scutaria* kills other coral species held in direct contact, but no reaction (neither aggressive killing nor immunological cytotoxic response) occurs when two *F. scutaria* coralla are held in contact (Hildemann *et al.*, 1975a, b, 1977; Chadwick, 1988). In preliminary experiments, we discovered that we could elicit a histocompatibility response by cutting the discoid skeletons with a rock saw and rejoining the resulting sections in various pairings and orientations of autogeneic, isogeneic, and allogeneic material. This technique allowed us to design experiments to explore three questions that are basic to our understanding of histocompatibility and regenerative processes in these corals.

Question 1: Do solitary corals display self/not-self histocompatibility responses similar to those observed in colonial scleractinians? Also, will grafts along cut surfaces react differently than grafts along uncut edges? Previous attempts involving intraspecific parabioses of *F. scutaria* failed to produce a histocompatibility or aggressive killing response at uncut edges (Hildemann *et al.*, 1975a, b, 1977; Chadwick, 1988).

Question 2: Does the presence or absence of a mouth influence regeneration or graft reactions? Presence of a mouth is known to influence survival and regeneration in other species of fungiids (Boschma, 1923; Chadwick and Loya, 1990), but nothing is known of the possible influence of the mouth on grafting response.

Question 3: Do naturally occurring aggregations of identical color-morphs of this species truly represent isogeneic clone-mates? These aggregations are believed to be derived asexually from the same anthocauli or ancestral corallum (Wells, 1954; Krupp *et al.*, 1993).

Fungiid corals are common throughout the Indo-Pacific (Hoeksema, 1989). Their free-living mode of existence

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enables them to colonize unstable rubble substrata (Hoeksema, 1988; Chadwick-Furman and Loya, 1992). *F. scutaria* is widely distributed from South Africa and the Red Sea in the west to Hawaii and the Tuamotu Archipelago in the east (Veron, 1986). The dense, discoid skeleton of this species has been shown to be an adaptation for hydrodynamic stability and abrasion resistance in turbulent, shallow water (Jokiel and Cowdin, 1976).

F. scutaria is a gonochoristic broadcast-spawner that releases gametes at dusk (Krupp, 1983). Spawning generally occurs between the second and fourth days following the full moon in the warmest months of the year (Krupp, 1983). The fertilized eggs develop into a typical planula larva within 12 h. The life cycle of fungiid corals has been summarized by Wells (1966) and Hoeksema (1989). After settlement, the planula begins to deposit skeleton and grows into a broadly attached cylindrical corallum called the anthocaulus. The oral end of the anthocaulus then expands radially, forming a disk-shaped structure called the anthocyathus. The resulting structure resembles a mushroom, hence the root word "fungi" was applied to these animals. The anthocyathus disk eventually breaks away from the anthocaulus stalk and begins life as a free-living, solitary corallum. The remaining anthocaulus tissues continue to produce additional anthocyathi, which break free and form additional coralla. Aggregations of identical color-morphs found on reefs are assumed to be clone-mates derived from a single anthocaulus (Wells, 1954, 1966).

Asexual reproduction occurs through budding from residual tissues of a damaged corallum (Bourne, 1887). Anthocaulus-like structures have also been observed arising from "dead" coralla of *Fungia* (Boschma, 1923; Krupp, 1983). Wells (1966) and Veron (1986) suggested that such buds are formed asexually from residual live tissue in damaged or dying parent coralla. Wells (1966) referred to these buds as "asexual anthocauli." The proliferation of new coralla from "dead" adult *F. scutaria* has recently been supported by direct evidence (Krupp *et al.*, 1993).

Materials and Methods

Fungia scutaria coralla were collected from shallow water (depth < 1 m) on patch reefs in the vicinity of Coconut Island, Kaneohe Bay, Hawaii, and held in continuous-flow aquaria supplied with nonrecirculating seawater from Kaneohe Bay. The aquaria were located outdoors in full natural sunlight, so the experimental environment was similar to that encountered in the shallow reef-flat habitat of this species.

The corals were cut with a circular rock saw. A continuous flow of seawater was directed at the diamond blade and the cutting area to prevent heating and drying of the tissues. After cutting, the corals were immediately returned to the continuous-flow aquaria. Regeneration in *Fungia* has long been known to be rapid (Kawaguti, 1937); the tissues grew and covered the exposed cut skeleton within 1 to 2 weeks. This species contains symbiotic zooxanthellae that produce enough photosynthetic product to allow the coral to grow in filtered seawater without heterotrophic feeding (Franzisket, 1969), so even cut sections without mouths will regenerate new tissues and deposit new skeletal material. There was no mortality of cut sections (either with or without mouths) or grafts in the months following the cutting process.

Sections cut for regeneration experiments were placed on plastic mesh racks and observed at regular intervals. The coral sections used in the various grafted combinations were held firmly together on notched acrylic plastic plates measuring 23 cm × 12 cm × 1 cm. The grafts were held securely in contact with monofilament nylon fishing leader (50-pound test). Monofilament strands were looped over the coral fragments and around the notched plastic plate, stretched by pulling the ends with hemostat clamps, and fastened on the back side of the plate with fishing leader crimps. Each graft pairing was labeled with a plastic tag. The plates were held off the bottom of the aquarium in a plastic rack at an angle of 60° to prevent accumulation of detritus or sediment.

Graft interactions were examined daily for the first month and subsequently at monthly intervals. Grafts were examined with the aid of a jeweler's magnifier during routine scoring. When needed, detailed examination was conducted with a platform stereomicroscope at 45× magnification. The term "tissue fusion" was applied to cases where tissues healed completely and became confluent between the two sections as observed under 45× magnification. In cases of "nonfusion," a boundary or gap persisted between the tissues of the two joined sections. Scoring tissues as fused or unfused was unambiguous, and we did not have to resort to histological techniques. At the conclusion of the experiments, the grafted skeletons were cleaned of all tissues by soaking in hypochlorite solution. After drying, the interfaces were examined for skeletal fusion. Sections that fell apart from each other when the monofilament ties were removed were scored as "unfused." Sections that had calcified heavily along the interface into a solid skeleton were termed "fused." Again, there was no ambiguity in the scoring of skeletal fusion.

Initially, we made six grafts of each type described below. Some types of graft pairings were increased in number to answer specific questions that arose during the initial experiments. For example, the first set of allografts showed a lack of cytotoxicity as well as a lack of fusion. Different genotypes of some colonial species show a wide range of rapid to slow and strong to weak reactions (Johnston *et al.*, 1981). Therefore we increased the numbers of pairings to rule out the possibility that we had selected only slow-

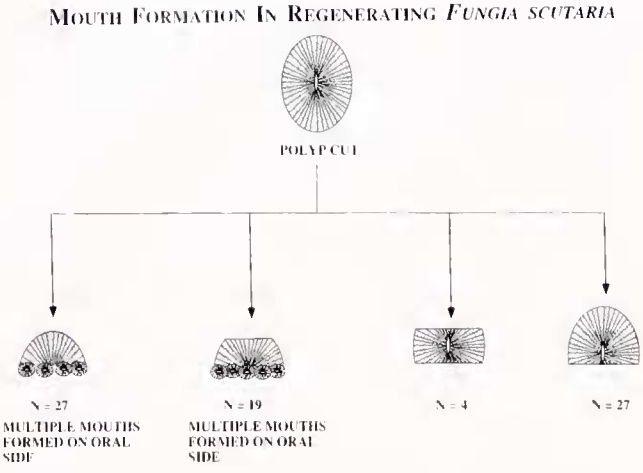


Figure 1. Mouth formation and regeneration in *Fungia scutaria* for cut sections with mouths, cut sections without mouths, and sections with two cut edges.

reactors in the first six grafts. The number was further increased to test the possible effects of different color-morph pairings. The original six grafts were sufficient to show a clear-cut response in many of the graft combinations.

The graft and regeneration experiments were designed to provide several types of information. The autograft experiments tested rates of tissue and skeletal fusion and the importance of cut versus uncut surfaces. Further, these experiments compared reactions between sections with mouths and sections without mouths. The allograft/isograft experiments were designed to provide information on histocompatibility reactions. They also allowed us to test the hypothesis that all identical color-morphs from the same aggregation are clone-mates, whereas corals taken from different reefs are allogeneic, even if they are of the same color-morph.

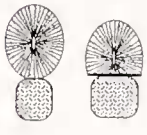
Regeneration experiments

Coralla were cut into sections with mouths and without mouths and with multiple cuts as shown in Figure 1. Sections were maintained in the continuous-flow microcosm aquaria on plastic mesh racks. During the 7-month regeneration period, we examined the fragments and noted the number and location of new mouths.

Autografts

Given a single corallum, four grafting orientations were of interest to us (Fig. 2, top). The first was a cut directly across the mouth region with subsequent regrafting in the same orientation. The second was a cut across the corallum outside of the mouth region with grafting in the original orientation. The third type of autograft was similar to the second, but we made an additional cut on the uncut outer edge, rotated the cut section 180°, and placed the two cut edges in contact. In the fourth case, the uncut

GRAFTING RESPONSE IN *FUNGIA SCUTARIA*

TISSUE SOURCE	AUTOGRAFT				ISOGRAFT					ALLOGRAFT			XENOGRAFT	
ORIENTATION														
SAMPLE SIZE	10	20	11	14	6	6	8	6	6	24	6	6	6	10
RESPONSE (% OF GRAFTS)														
FUSION														
TISSUE	100%	100%	91%	22%*	100%	100%	25%*	0	0	0	0	0	0	0
SKELETON	100%	100%	91%	0	100%	100%	0	0	0	0	0	0	0	0
NO RESPONSE	0	0	9%	78%	0	0	75%	100%	100%	100%	100%	0	0	0
ABNORMAL TISSUE	0	0	0	0	0	0	0	0	0	0	0	100%	0	0
KILLING	0	0	0	0	0	0	0	0	0	0	0	0	100%	100%

*OCCASIONAL TISSUE CONNECTIONS—NOT COMPLETE FUSION.

Figure 2. Summary of grafting results for autografts, isografts, allografts, and xenografts of *Fungia scutaria* in various orientations.

edge of the cut piece was rotated 180° and placed in contact with the opposite uncut free edge of the parent corallum.

Isografts

Aggregations of single color-morphs found on the reef have long been assumed to be clone-mates derived from a single ancestral anthocaulus through asexual formation of multiple anthocyathi. *F. scutaria* in Kaneohe Bay display different combinations of tentacle color (green or brown), mouth color (white, purple, brown, or green), and disk color (brown, mottled white-brown, or violet). Pairs of the same color-morphs taken from within such natural aggregations were used in all isografts. The corals were cut on the rock saw and grafted in the five configurations shown at the top of Figure 2. In the first configuration, a section with a mouth was joined to a section that lacked a mouth and had been cut from a putative clone-mate. The second type of isograft was made by grafting two sections that lacked mouths and had been cut from two presumed clone-mate coralla. A third type joined two mouth-bearing sections along their cut edges. The fourth was the same as the third, but joined along the free uncut edges. The fifth type of isograft joined two sections without mouths at the uncut free margins.

Allografts

Allografts were made between corals taken from different reefs and presumably derived from different planulae settlements. Three types of allografts were made (Fig. 2, top). The first type consisted of grafting sections from two different corals, but with both sections having mouths ($n = 24$). Allografts were made between sections containing mouths for identical color-morphs taken from different reefs ($n = 12$) and from pairings of different color-morphs taken from the same reef ($n = 12$). In the second type, only one of the pair had a mouth ($n = 6$); in the third type, neither had a mouth ($n = 6$).

Xenografts

As a control, 16 xenograft pairings were made between *F. scutaria* and the colonial reef coral *Montipora verrucosa* at cut and uncut edges. (Fig. 2). A number of previous studies show rapid killing of *M. verrucosa* by *F. scutaria*. These xenografts served to demonstrate whether the killing response was active during our experiments.

Results

Regeneration experiments

The freshly cut skeletons (Fig. 3a) healed within 1 to 2 weeks. Each section with a mouth began to regenerate septae on the cut surface within 60 days (Fig. 3c). After 7 months, no additional mouths had formed on the 31 sections that initially had a mouth (Fig. 1). Multiple mouths formed within 45 days on all 46 sections that initially lacked a mouth (Fig. 1). At 90 days, many of the mouth areas started to form into anthoblasts and began to separate (Fig. 3b) in a manner reminiscent of polyp formation from an anthocaulus (Fig. 3d). In all 46 cases, the new multiple mouths formed along the cut margin proximal to what had been the mouth area of the original corallum. Areas distal from the original mouth area (on sections with and without a second cut) did not develop new mouths (Fig. 1).

Autografts

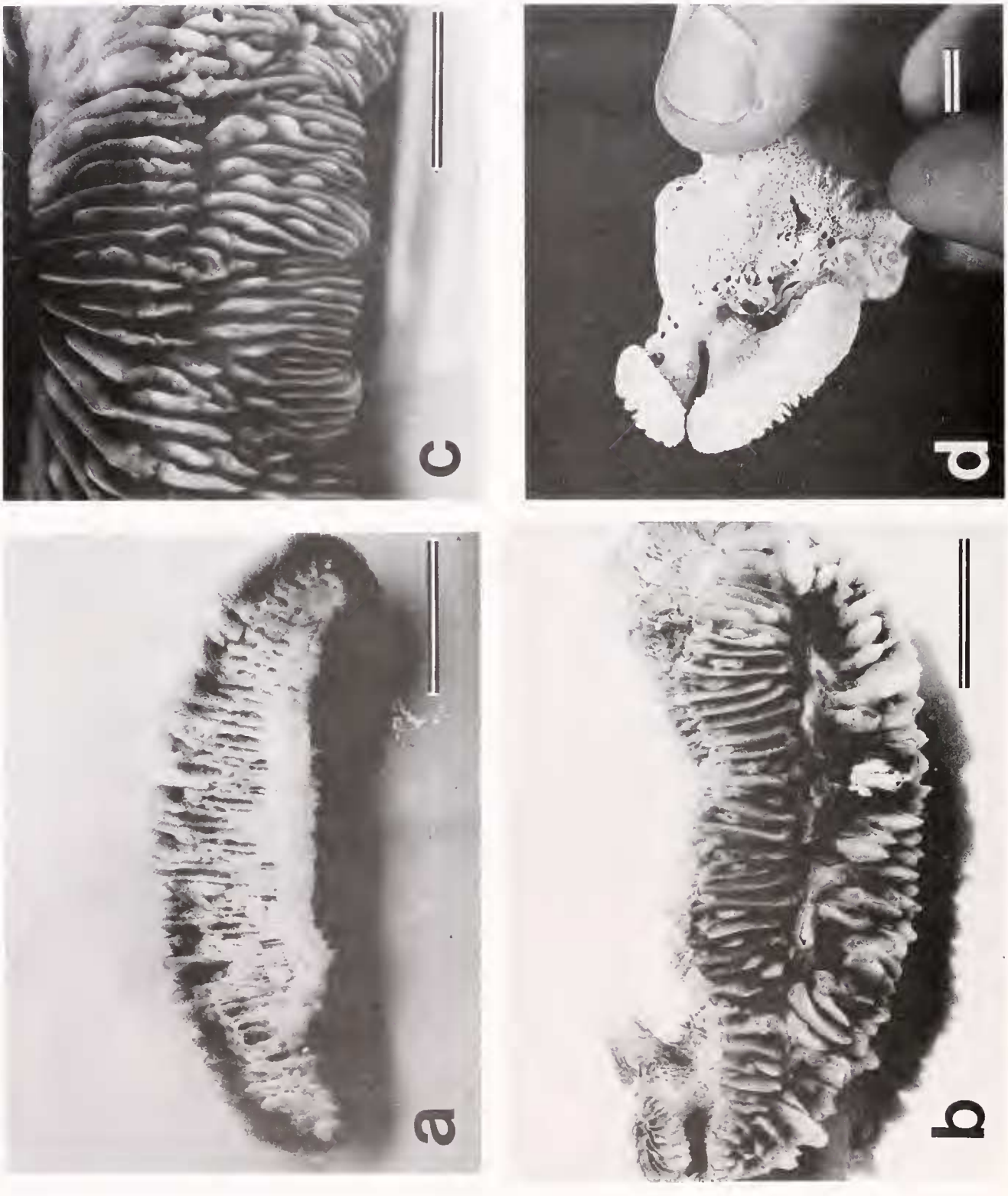
All autografts joined along cut surfaces in their original orientation showed complete tissue and skeletal fusion (Figs. 2, 4a, 4c). Fusion of tissue was rapid, with confluences observed within 48 h. Within 60 days, the skeletons were fused to the point that the sections would hold together without support. One of the autografts made at cut surfaces in the rotated orientation did not fuse. Autografts made with contact along the uncut outer free margin did not show skeletal or tissue fusion (Figs. 2, 4b, 4d). In some cases we noted occasional stringlike tissue connections across the graft interface, but these did not persist for more than a few days.

Isografts

All isografts between a section with a mouth and a section without a mouth fused completely if joined along the cut edge, but did not fuse if joined at the uncut free outer edge (Fig. 2). Isografts along cut edges between two mouth-containing sections did not show any skeletal fusion. As in the case of autografts joined at the free edge zone, we noted occasional stringlike tissue connections at the interface. Apparently, recognition was occurring, as evidenced by the limited and nonpersistent connections. However, these connections dissipated, and fusion did not occur between two sections containing mouths. In contrast, grafts between two fragments without a mouth that were joined along the cut surface fused completely and formed a new mouth at the interface (Figs. 2, 5b).

Allografts

Allografts showed no signs of tissue fusion or skeleton fusion, regardless of combination or orientation of the graft (Figs. 2, 5a). Also, there was no sign of cytotoxic killing between the two tissue types. Polyps attempted to push away from each other by "inflating" the coelenteron with water. Mesenteries were extruded, but no tissue damage was observed on live material viewed with a ster-


a
b
c
d

eomicroscope at 45×. Pairings between identical color-morphs taken from different reefs did not fuse. Graft combinations using pairings of different color-morphs did not show heightened reactions compared to pairings with the same color pattern from different reefs. Abnormal hyperplasia (not necrosis) and mouths appeared in the fragments paired cut edge to cut edge (*e.g.*, Fig. 5a), but tissue and skeletal fusion did not take place.

Xenografts

Concurrent control xenografts of *F. scutaria* paired with the colonial coral *M. verrucosa* resulted in killing of the *M. verrucosa* along the interface within 3 days. The *F. scutaria* maintained a 1-cm-wide tissue-free zone throughout the 7-month experiment. This control demonstrated the presence of the killing response in our experimental material. The observed lack of cytotoxicity or aggressive killing in autografts, isografts, and allografts of *F. scutaria* was not due to lethargy among the experimental corals.

Discussion

Results of these grafting experiments provide the first evidence of a self/not-self histocompatibility recognition system in a solitary reef coral. The response of *Fungia scutaria* is analogous to that observed in colonial corals (*e.g.*, Hildemann *et al.*, 1975a, b, 1977) in that allografts and presumed isografts fused, but allografts did not fuse. No cytotoxic killing was noted in allografts. Unique and previously unreported observations for *F. scutaria* include the observation that isogeneic mouth-containing individuals do not fuse at cut edges, but isogeneic sections without mouths will fuse. Also, isogeneic grafts do not fuse along the intact free edge of the solitary corallum, as shown by isograft and allograft pairings involving cut *versus* uncut edges.

Grafts between sections from different coralla taken from the same aggregation of *F. scutaria* fused at the same rate and in the same manner as autografts. Scientists have previously suspected that such "families" of *Fungia* probably represent clone-mate aggregations derived from multiple asexual budding from a single ancestral anthocaulus (*e.g.*, Wells, 1954). An alternate hypothesis is that such aggregations are the result of a mass settlement of sibling planulae that each gave rise to an anthocaulus and anthocyathi.

Recently, it has been shown that successful recruitment of sexually derived planulae of *F. scutaria* on the reefs of Kaneohe Bay is rare (Fitzhardinge, 1993; Krupp *et al.*, 1993). More than a decade has passed since spawning of gametes and sexual production of planulae were first observed and described for this species (Krupp, 1983). During the initial study and in many subsequent attempts, D. Krupp (pers. comm.) and other researchers have been unable to induce settlement in planulae of *F. scutaria*. A variety of substrata and environmental regimes have been presented to the planulae, but they have not settled and formed anthocauli. Larvae of the other common Hawaiian coral species readily settle under laboratory conditions, but it seems that the conditions required for settlement of *F. scutaria* are highly specific. We have not found new *F. scutaria* anthocauli developing on fouling plates or on blocks, reef rock, or other substrata placed in the bay to measure recruitment over the years. A long-term study designed to measure coral recruitment in Kaneohe Bay has recently been completed (Fitzhardinge, 1993). About 170 concrete blocks were set in various shallow-water reef environments and monitored for coral recruitment over a period of 3 years. Thousands of settlements of all other common Kaneohe Bay coral species were recorded, but only a single *F. scutaria* anthocaulus was noted. Even the anthocaulus-like structures found attached to natural reef substrates (other than dead parent coralla) often are asexually derived. Close examination of these structures reveals that many arise from highly eroded and encrusted *F. scutaria* coralla that have been incorporated and cemented into the reef matrix. Apparently, asexual reproduction is the dominant means of proliferation of *F. scutaria* in Kaneohe Bay (Krupp *et al.*, 1993).

Given the well-documented importance of asexual reproduction in this species and the rarity of successful sexual reproduction, we conclude that the most parsimonious explanation for the occurrence of aggregations of identical color-morphs is asexual proliferation of coralla. It is hard to imagine how aggregations of isogeneic color-morphs could be achieved by multiple planulae settlements at one site.

Results of the isograft experiments are consistent with the asexually derived clonal hypothesis. Identical color-morphs taken from different reefs, however, were allogeneic and did not fuse. The usefulness and interpretation of histocompatibility responses as a measure of genetic structure of populations is debated (*e.g.*, Curtis *et al.*, 1982;

Figure 3. All scale bars = 1 cm. (a) Freshly cut section of *Fungia scutaria*. (b) Regeneration of mouths from a section cut without a mouth after 7 months. Note formation of a new anthocyathus from the former aboral surface. (c) Regenerated septae on a section with a mouth after 7 months. (d) Two anthocyathi sprouting from isogeneic tissue (anthocauli). Note that isogeneic tissues of the two anthocyathi do not fuse at the edges.

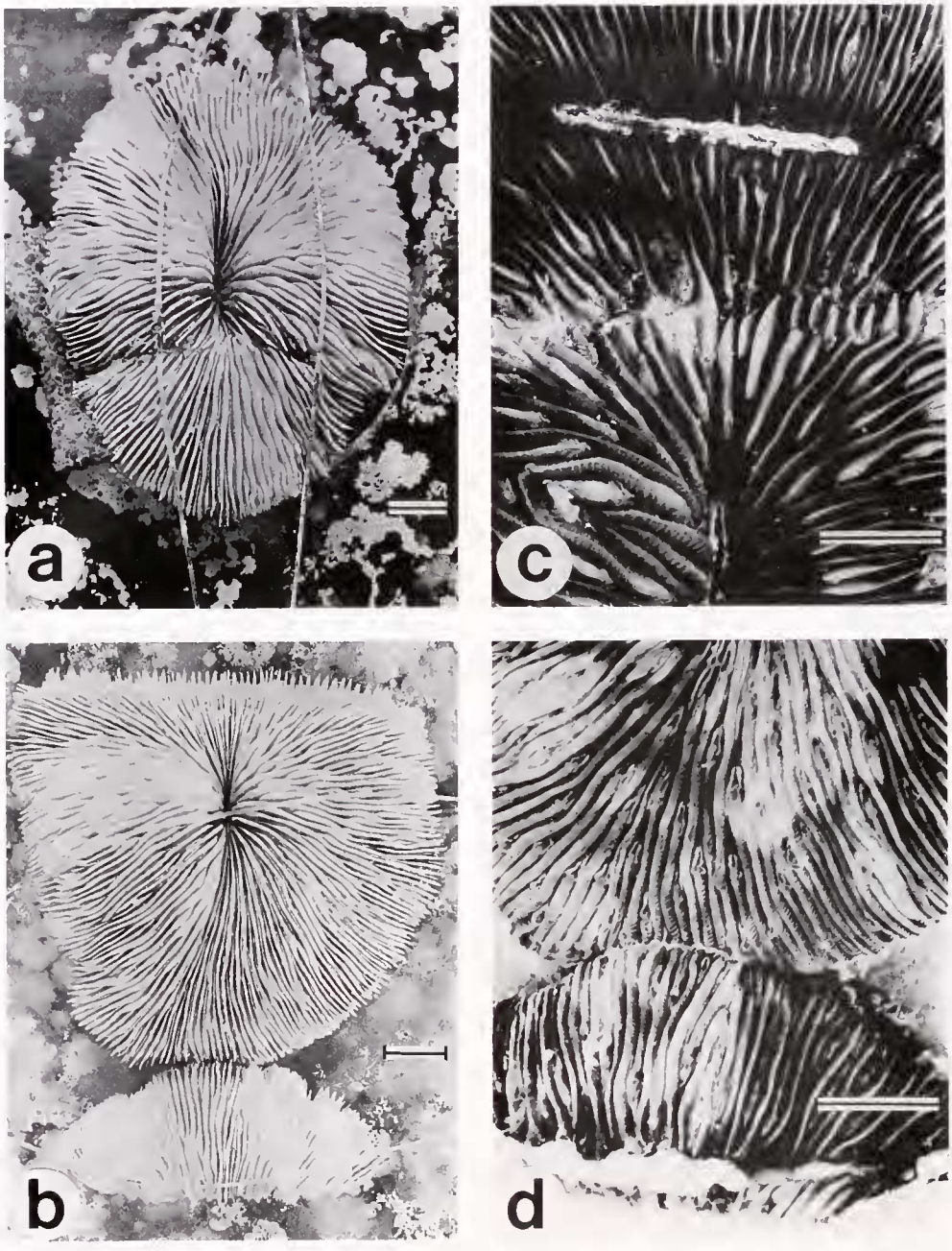


Figure 4. All scale bars = 1 cm. (a) Cleaned skeleton of cut edge to cut edge autograft of *Fungia scutaria* showing fusion of skeleton after 7 months. (b) Cleaned skeleton of uncut edge to uncut edge autograft showing no fusion after 7 months. (c) Autograft fusion of tissues at 7 months along rejoined cut edge. (d) Autograft nonfusion of tissues in uncut edge to uncut edge at 7 months.

Rinkevich and Loya, 1983; Willis and Ayre, 1985; Heyward and Stoddart, 1985; Hunter, 1985; Grosberg, 1988). Nevertheless, in the case of *F. scutaria*, our results are consistent with the notion that aggregations of identical color-morphs are isogeneic.

Organization of tissues in *F. scutaria* into an anthocyathi begins with the formation of a mouth. This is true for development of anthocyathi from anthocauli, formation from fragments without mouths (Fig. 3d), and proliferation of coralla from damaged or dying coralla. Each new mouth becomes a center of polyp development. An edge zone forms around each mouth area, leading to the eventual separation of polyps from each other and from the parent anthocaulus if they are to become solitary

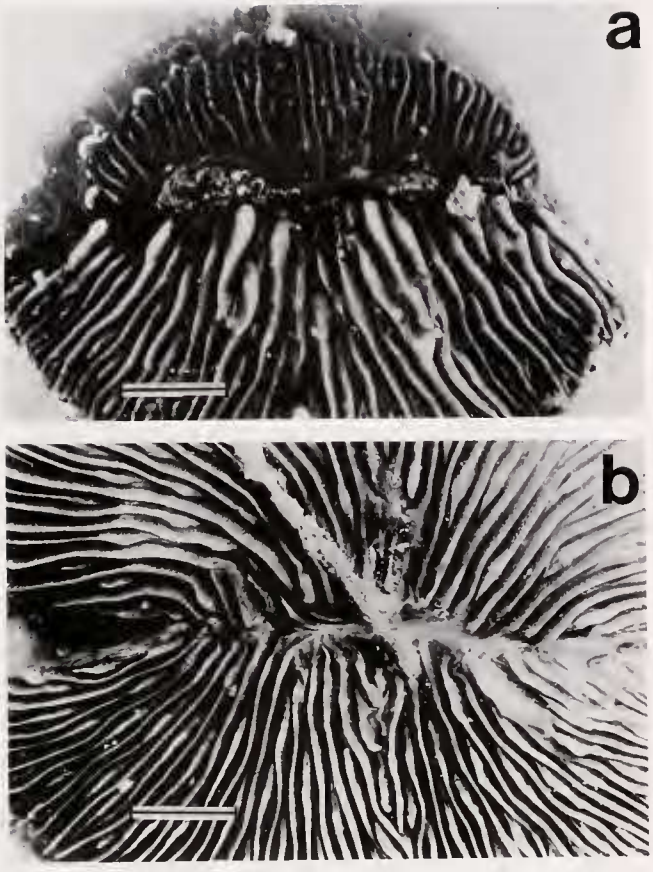


Figure 5. All scale bars = 1 cm. (a) Allograft between two mouthless fragments of *Fungia scutaria* one year after grafting. Note lack of fusion and formation of abnormal hyperplasia along interface. (b) Isograft between mouthless sections one year after grafting. Note fusion of tissues and formation of new mouth along the interface.

polyps. Polyps of *F. scutaria* must possess a mechanism that initially causes separation of the corallum from parent tissue. Juvenile clone-mate anthocyathi on the same anthocaulus will separate even though connected at the base by continuous tissues and touching along the edge zone (Fig. 3d). Once the mouth has formed, there must be further development leading to the separation of a solitary coral from the parent tissue.

Formation of buds from tissues lacking a mouth leads to rapid proliferation of new coralla from parent anthocauli as well as from damaged or senescent coralla. Each bud in turns leads to formation of an anthocyathi. Perhaps the same process that causes polyp separation is responsible for the prevention of refusion of clone-mates once they have separated. "Families" of *F. scutaria* derived from a common anthocaulus do not fuse into a single isogeneic mass (Chadwick, 1988), as would occur with colonial clone-mates on a reef (*e.g.*, Jokiel *et al.*, 1983).

Theories on the mechanisms controlling development have been proposed and tested among hydrozoan coelenterates (*e.g.*, Babloyantz and Hiernaux, 1974), but such studies are generally lacking among the anthozoans. Architectural methods used to describe growth in tropical trees have been used to describe coral growth, including *Fungia* (Dauget, 1991). Fungiid corals provide an attractive experimental model because members of this family show considerable diversity in structure and developmental pattern. For example, the free-living solitary coral *Diaseris fragilis* reproduces asexually by breaking into wedge-shaped fragments, each of which later forms a mouth and develops into a discoid corallum (Yamashiro *et al.*, 1989). The fungiid *Sandalolitha robusta* has multiple mouths, but its early development is similar to that of *Fungia* (Yamashiro and Yamazato, 1987). The anthocyathus detaches from the anthocauli at an early stage and follows a free-living existence thereafter. The number of mouths and tentacles on the disk continues to increase, however, leading to the polystomatous condition. The anthocyathus continues to regenerate additional polyps, which also detach. Unlike *F. scutaria*, *S. robusta* does not show the influence of the mouth in preventing formation of additional mouths.

Results of the regeneration experiments are consistent with the classic observation that extensive budding in *F. fungites* can be induced by selectively killing the mouth region with putty (Boschma, 1923). In our experiments, all sections cut without a mouth formed new mouths, and all sections cut containing a mouth did not form mouths. Location on cut fragment is important in mouth formation. Sections without mouths cut along a second line parallel to the first cut always regenerated multiple mouths along the cut edge proximal to the former mouth area. During the first stage of polyp formation, multiple mouths proliferate from cut sections in a manner analogous to that observed in anthocauli and damaged coralla.

Acknowledgments

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